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The neurocognitive basis of reading single words as seen through early latency ERPs: A model of converging pathways

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ABSTRACT

This paper first provides a brief review of the functional neuroanatomy of reading single words, focusing on the lexical and phonological routes. Next, early (defined as peaking prior to 350 ms) reading event-related potential components are summarized. A comprehensive effort is made to organize existing observations into a coherent scheme and commentary is made on terminology. Proposals are made regarding the cognitive function reflected by each ERP component and the associated generator sites. The overall framework constitutes a neurocognitive model of reading and demonstrates how the high temporal resolution of event-related potentials can provide additional insights into the reading process beyond those available from behavioral and neuroimaging studies, with a special focus on how the two pathways implied in reading are coordinated. The present model suggests that there are two such coordinating operations, convergence processes during an initial information burst and resonance processes during an extended harmonization process that follows.

Despite the importance of language to the understanding of current issues of education and ultimate questions of the nature of human thought, the study of reading processes persists in a contentious state. While there is broad agreement on some aspects of reading, such as the presence of both orthographic (the letter sequence) and phonological (the sound sequence corresponding to the letter sequence) codes, basic questions regarding their implementation, relative importance, and time course remain under debate. The development of neuroimaging techniques has provided some helpful insights into the architecture of language processing that have helped guide and constrain cognitive models but they lack crucial information on the time course of the observed neural activity.

Event-related potentials (ERPs) have the promise of helping resolve some of these issues by providing timing information. This relatively new literature provides a rich source of information but thus far is fragmented, with numerous ERP components reported in a bewildering array. This review will seek to provide a systematic overview of these findings and consideration of their implications for cognitive models. The ultimate goal is to seek to develop a neurally based model of language comprehension that is informed by the event-related potential literature. This effort will differ from a previous such effort (Barber and Kutas, 2007) in that it will focus on cataloging ERP components and assessing what they reveal about the time course of putative neurocognitive functions whereas the prior review focused on the time course of psycholinguistic variables and their implications for the architecture of connectionist models.

In order to simplify the task, this effort will focus on reading comprehension as opposed to speech comprehension. Also, although some sentence studies will be cited, this review will not address sentence-specific processing such as syntax or discourse. It will also set aside the magnetoencephalography (MEG) literature (e.g., Simos et al., 2002) for a future treatise for space reasons and because it would distract from the focus of this special issue, which is on ERP studies. First a base neural model of reading comprehension will be outlined and then the ERP literature will be reviewed in an effort to develop a neurocognitive timeline of reading comprehension (Table 1). Finally, there will be some speculations on implications of these findings for theoretical models, with a special focus on how the two pathways are coordinated.

1. A neurocognitive model of early reading comprehension

The literature on reading comprehension in both the cognitive and neuroimaging literatures is quite complex and therefore a full treatment of this topic lies outside the scope of the present review. Instead, this section will describe one version of a neurocognitive

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Table 1
Summary table of early latency reading comprehension event-related potentials

Peak latency	ERP	Anatomy	Function
100	P100	Extrastriate occipital	Low-level perception
150	P150-Cz	Inferior occipital cortex	Word shape
150–180	N170-PO7	Visual word form area	Bigram analysis
200	N2-P3	Fusiform semantic area	Lexical access
250	Recognition potential	Language formulation area?	Lexical selection and orthographic-phonological mapping
250–350	MFN/N300/P2/PMN	?	Phonological analysis?
300–350	N300-T3	Left supramarginal gyrus	Phonological store

reading architecture that is able to provide a framework for the succeeding ERP review.

To start with, the most relevant cognitive model of reading is the influential dual-route cascaded (DRC) model of visual word recognition (Coltheart et al., 2001). In this model, there are essentially two major pathways from the printed word to semantic access. After initial low-level perceptual analysis and identification of the letters, the information is passed along to the lexical and phonological pathways. The lexical pathway begins with orthographic analysis of the percept, and then the orthographic code is identified in the orthographic input lexicon. The result is then passed on to the semantic system. If the word is not present in the orthographic input lexicon, a less efficient pathway is available that first involves a grapheme–phoneme rule system to generate a phonological representation which is then passed on to a response buffer. From there it can be passed to a phonological output lexicon where the word can be identified. From there it can be passed on to the semantic system. Reciprocal connections between the orthographic input lexicon and the phonological output lexicon allow for the two pathways to interact. An important characteristic of this model is that although it highlights discrete stages of the reading process, it explicitly acknowledges that partial information is output from each stage, resulting in a cascaded or continuous flow dynamic (see also Coles et al., 1985; Eriksen and Schultz, 1979).

Turning to neural models of reading comprehension (Fiez and Petersen, 1998; Jobard et al., 2003; Joseph et al., 2001; Price, 2000; Price and Mechelli, 2005; Vigneau et al., 2006), findings thus far are largely compatible with the DRC but require some elaborations on it.

1.1. *Lexical pathway*

Evidence suggests the existence of a lexical pathway running along the inferior surface of the temporal lobe. One model suggests that along this pathway the visual percept of the word is increasingly abstracted (Dehaene et al., 2005; Vinckier et al., 2007). The ultimate form of this representation would be a lexical-level representation that is independent of physical stimulus characteristics like case, of a sort that has been inferred by behavioral studies (Reicher, 1969; Wheeler, 1970).

Three areas in this region have received special attention. The first is the inferior occipital cortex (IOC) encompassing the inferior occipital gyrus and lingual gyrus. The laterality of this word sensitive area has varied between left-lateralized (Madden et al., 2002; Petersen et al., 1990; Puce et al., 1996), right-lateralized (Dehaene et al., 2001), or bilateral (Indefrey et al., 1997). While an initial report (Petersen et al., 1990) suggested that it contained a lexical-level visual word form area (being more active to orthographically regular letter strings than consonant strings), subsequent studies have not supported this conclusion. For example, one study (Tagamets et al., 2000) actually reported the opposite pattern, namely that the consonant strings produced more activation than words. It is likely that this region is instead responding to global word shape (Indefrey et al., 1997; Mechelli et al., 2000) and is therefore responsive to changes in perceptual characteristics such as case (Dehaene et al., 2001) and letter length (Valdois et al., 2006). Functionally, the IOC is therefore more likely to be part of the initial feature and/or letter analysis prior to the two pathways than to be part of the lexical pathway as initially thought.

The second area has been dubbed the visual word form area (VWFA). It is located midway along the fusiform gyrus, anterior to the IOC, and is strongly left-lateralized to the extent that its laterality is independent of visual field presentation (Cohen et al., 2002). The VWFA appears to mediate orthographic analysis at the bigram level as part of a series of processing steps (Dehaene et al., 2005). Striking evidence for its role in the reading process has been provided by a case study of brain surgery case before and after this area was removed (Gaillard et al., 2006). Support for the bigram hypothesis comes from the finding (Binder et al., 2006) that VWFA activity is correlated with bigram frequency and that this is the case even for non-orthographic non-words. Further evidence that the VWFA mediates (sub)lexical-level analysis is that the VWFA has been shown to be case-insensitive in repetition priming, as one would expect for a representation that has been abstracted from the original percept (Dehaene et al., 2001, 2004). The VWFA also showed evidence of abstraction in that it was not affected by retinal position (Dehaene et al., 2004) and in that it was more responsive to orthographic regularity than to whether the stimuli were presented in perceptually unfamiliar mixed-case format (Polk and Farah, 2002). Further information can be found elsewhere in a review of lateralized orthographic processing (Dien, submitted for publication).

The third area is located anterior to the VWFA, along the anterior fusiform gyrus, and is one of three areas cited (Jobard et al., 2003) as displaying evidence of responding to semantics, both for words and for object pictures (Moore and Price, 1999). Furthermore, it shows greater activation to the lexical kanji script than to the phonological kana script (Nakamura et al., 2005). The term fusiform semantic area or FSA has been suggested to facilitate discussion of this area (Dien et al., in press). A study of semantic priming (Gold et al., 2006) reported that it responded to automatic spreading activation (ASA) effects, providing further evidence of its sensitivity to this level of processing. Despite the sensitivity to semantic manipulations (e.g., Moore and Price, 1999), it is suggested here that it may correspond best with the DRC's orthographic input lexicon. This suggestion is made based on the reasoning that given the apparent hierarchic gradient of processing along the inferior temporal lobe (e.g., Vinckier et al., 2007), one would expect a whole-word level of lexical analysis to follow the sub-lexical level of the VWFA. Furthermore, ascribing the complexities of semantic knowledge to such a small patch of cortex seems implausible. The ASA effects (Gold et al., 2006) could be explained more parsimoniously as being the result of lexical-level associations rather than semantic-level. Although one might therefore argue for a name like Fusiform Lexical Area, such a name would have a possibly unsupportable implication that it only